Odonatologica 14 (3): 201-210 *September 1, 1985*

THE LIFE CYCLE OF *ARGIA VIVIDA* HAGEN: DEVELOPMENTAL TYPES, GROWTH RATIOS AND INSTAR IDENTIFICATION (ZYGOPTERA: COENAGRIONIDAE)

M. LEGGOTT and G. PRITCHARD[1]
Department of Biology, University of Calgary, 2500 University Drive N.W.,
Calgary, Alberta T2N 1N4, Canada

Received and Accepted February 19, 1985

Eggs were hatched in the laboratory and larvae reared to the final instar. Three developmental types were recognized (12, 13 and 14 instars) and there was a positive correlation between growth rate, final size, number of instars and temperature between 15 and 25° C. These factors, plus intra-instar variation, allow only the 1st, 2nd, 3rd, and final instars to be identified with certainty. The number of antennomeres, metathoracic wing pad length, and head width were useful in assigning larvae to instar. Head width growth ratios decreased as larvae grew; the average growth ratio was 1.24.

INTRODUCTION

The genus *Argia* is limited to the New World, where its highest species diversity occurs in Central and northern South America. PRITCHARD (1982) has reviewed the distribution of the genus and discussed possible mechanisms which have allowed colonization of North America. The most northerly ranging species is *A. vivida* Hagen which is distributed throughout western North America from Mexico to southern Alberta and British Columbia. It occurs in geothermally heated streams over most of its range and is typical of such habitats in the north, although WHITEHOUSE (1941) reported it from Field, B.C. and it occurs at Penticton, B.C. (Cannings, Pritchard, Leggott, unpublished observations) where there are no hot springs.

The ecology of this species is currently under intensive study (PRITCHARD & PELCHAT, 1977; PRITCHARD, 1980, 1982), and the present paper provides a basic description of the life cycle as a foundation for this ecological work.

---

[1] Author for correspondence

METHODS

Field Sites

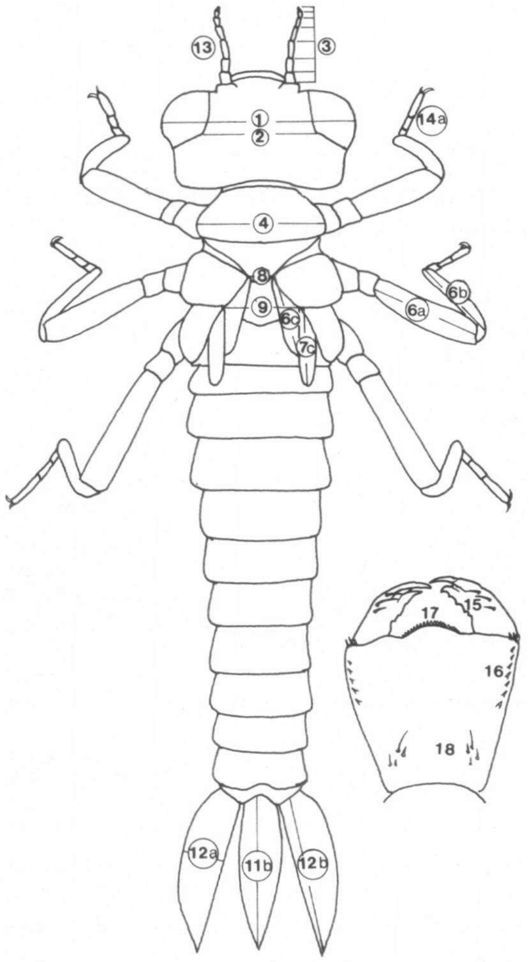

Fig. 1. Some of the characters used in the instar analyses. Numbers correspond to those in Table 1. All measurements were for the maximum distance of the area in question.

Mating pairs and larvae of *A. vivida* were collected at 2 sites: Cave & Basin Hot Springs, Banff, Alberta (51° 10'N, 115° 34'W); and Deep Creek, Idaho (42° 24'N, 112° 44'W). Both sites are in geothermal areas but the influence of geothermal activity on the two sites differs considerably. The water at the Cave & Basin site is maintained at a fairly constant 26° C year-round, whereas Deep Creek varies from 0° C with ice cover for 3 months in winter to a summer maximum of 33° C and daily fluctuations of 15-20° C. The annual degree-day accumulations above 0° C in the streams at the two sites are 9500 and 2560 respectively, but air temperatures are higher at Deep Creek than at the more northerly Canadian site.

Laboratory Procedures

In order to determine which larval characters might provide data with which to separate individuals into instars, 30 characters were examined on 150 larvae in various instars collected from the Cave & Basin (Tab. I; Fig. 1). Characters such as dental formula on the mandibles, setal formula on the postero-lateral margins of the head, prothorax and abdominal segments, setal formulae on the caudal lamellae, and lengths of the gonapophyses were not used because they were difficult to quantify. After this preliminary analysis all but 11 of the characters were rejected from further study because they were repetitious or too invariant.

These 11 characters were studied on larvae reared in the laboratory. Mated females oviposited into moist filter paper in laboratory cages kept at 22° C and a photoperiod of L:D 14:10. Eggs were transferred in batches of 20 to individual petri-dishes, covered with dechlorinated water, and placed

Table I

Characters used in the instar analyses. Starred (*) characters are those used in the final analysis

(1) Head width*
(2) Intraocular distance
(3) Antennomere lengths
(4) Prothorax width
(5) Prothoracic a) tibia* b) femur lengths
(6) Mesothoracic a) tibia b) femur c) wingpad lengths
(7) Metathoracic a) tibia b) femur c) wingpad* lengths
(8) Distance between proximal tips of mesothoracic wingpads
(9) Distance between proximal tips of metathoracic wingpads
(10) Prementum a) width b) length*
(11) Median caudal lamella a) width b) length
(12) Lateral caudal lamella a) width b) length
(13) Number of antennomeres*
(14) Number of a) prothoracic* b) mesothoracic* c) metathoracic* tarsomeres
(15) Number of palpal setae* on prementum
(16) Number of marginal setae* on prementum
(17) Number of median lobe teeth* on prementum
(18) Number of premental setae
(19) Number of tarsal setae
(20) First appearance of gonapophyses

at constant temperatures (5-35° C in 5° C intervals) and L:D 14:10 until they hatched. Instar 2 larvae were transferred individually to petri-dishes filled with deionized water and redistributed amongst the constant temperatures with equal numbers of larvae from each of the egg temperatures at each of the larval temperatures. Each dish was provided with an excess of appropriately-sized enchytraeid worms and was checked at 3-day intervals (every day at 30 and 35° C) at which time uneaten food was removed and replaced, exuviae were removed and preserved in 4% formaldehyde, and head-widths of newly moulted individuals were measured. The water was replaced at regular intervals. Rearing to the final larval instar was successful only at 15, 20 and 25° C.

All measurements and counts were made under a stereo-microscope on exuviae, except for head-width which is difficult to measure on exuviae because of the ecdysial split. Measurements were made to the nearest 0.01 mm.

RESULTS

The eggs of *Argia vivida* are ellipsoidal, approximately 4X as wide as long, and pointed at the anterior pole. There is a faint sculpturing of the chorion except at the anterior end. At oviposition, the eggs are light cream colored with a translucent chorion, but 3-4 hr later they turn black, although the chorion remains translucent. Eggs which do not change color, do not develop. At hatching, the chorion splits around the anterior end and the cap remains attached at a point below the larval head. This type of hatching is often observed in insects which lack an egg burster (HINTON, 1981).

The first instar (or prolarva) emerged from the egg shell by repeated dorsoventral body movements, aided by posteriorly-directed setae on the thorax and abdomen. The prolarva remained attached to the egg by its caudal lamellae until the first instar cuticle ruptured and the second instar emerged, leaving the instar 1 cuticle attached to the egg shell. At 35° C a few larvae completed hatching and became detached from the egg shell but remained in the instar 1 cuticle. All subsequent molts were similar to the first, except that the exuvia often remained attached to the caudal lamellae for a short period of time; at 10 and 15° C it was often 1-2 days before it was completely shed.

The number of instars varied, with 3 developmental types recorded. Of the 18 larvae which attained the final instar, 12 had 13 instars, 5 had 12 instars, and 1 had 14 instars.

Table II

Character variation in the 13 instar developmental type (Measurements are expressed as x ± 1SD, with the range in parentheses; — numbers of tarsomeres are given in the order pro/meso/metathoracic)

Instar	Head width	Growth ratio	Prothoracic tibia length	Prementum length	Antennomeres	Tarsomeres	Palpal setae	Marginal setae	Median lobe teeth
2	0.36±0.01 (0.34–0.38)		0.20+0.02 (0.13–0.28)	0.25±0.01 (0.23–0.26)	3	1/1/1	1+1	1+1	2
		1.31							
3	0.47±0.03 (0.40–0.48)		0.25±0.05 (0.14–0.38)	0.33±0.02 (0.30–0.38)	4	1/1/1	1+1	1+1	8,9,10,12
		1.30							
4	0.61±0.04 (0.51–0.56)		0.43±0.07 (0.35–0.57)	0.46±0.05 (0.35–0.57)	5	2/2/2	1+1	1+1, 1+2, 2+3	9,10,11,12,13
		1.28							
5	0.78±0.05 (0.68–0.88)		0.56±0.10 (0.40–0.73)	0.54±0.08 (0.40–0.73)	5	2/2/2 or 2/2/3	1+1	2+2, 2+3, 3+3, 3+4	11,12,13,14,15,16
		1.27							
6	0.99±0.07 (0.86–1.14)		0.71±0.14 (0.49–0.93)	0.70±0.10 (0.49–0.93)	6	2/3/3 or 3/3/3	1+1	3+3, 3+4, 4+4, 4+5 5+5, 4+6, 7+6	12,14,15,16,17,18
		1.26							
7	1.25±0.09 (1.06–1.52)		0.84±0.19 (0.54–1.11)	0.89±0.21 (0.61–1.17)	6	3/3/3	1+1, 2+2	3+4, 4+5, 5±5, 5+6 5+7, 6+6, 7+6, 7+8 8+6	17,18,19,20,21,23
		1.22							
8	1.52±0.10 (1.30–1.86)		1.05±0.23 (0.70–1.41)	1.01±0.27 (0.73–1.40)	7	3/3/3	1+1, 2+2	5+6, 7+6, 6+8, 7+7 7+8, 8+8, 9+7, 8+9 9+9	19, 20, 21, 22, 23
		1.22							
9	1.86±0.13 (1.60–2.20)		1.27±0.31 (0.81–1.70)	1.22±0.31 (0.90–1.60)	7	3/3/3	1+1, 2+2, 3+2	7+6, 7+8, 7+9, 8+9 10+8, 10+10, 10+11 11+11, 11+12	21,22,23,24,26,27
		1.22							
10	2.26±0.25 (2.01–2.66)		1.56±0.30 (1.20–1.90)	1.57±0.25 (1.30–1.85)	7	3/3/3	2+2, 3+2, 3+3	9+9, 9+11, 11+11 11+12, 11+13, 13+14 14+14, 14+15	25, 26, 28, 29, 30,32 34
		1.18							
11	2.67±0.21 (2.24–3.04)		1.72±0.22 (1.50–2.05)	1.80±0.17 (1.60–2.00)	7	3/3/3	2+2, 3+2, 3+3	11+10, 11+11, 11+12 13+13, 14+15, 15+17	26,28,31,32,34,35 36
		1.15							
12	3.08±0.17 (2.80–3.36)		1.94±0.26 (1.70–2.30)	1.98±0.10 (1.75–2.10)	7	3/3/3	2+2, 2+3, 3+3 2+4, 3+4, 4+4 4+5	12+14, 13+14, 13+15 14+15, 15+15, 16+17 17+19	30,34,35,38,39,40
		1.19							
F	3.66±0.11 (3.30–4.20)		2.36±0.37 (1.95–2.80)	2.25±0.26 (1.90–2.60)	7	3/3/3	3+3, 3+4, 4+4 5+4, 5+5, 6+5 7+5, 8+5	13+14, 13+15, 14+16 16+16, 16+17, 17+18 16+20, 17+20	36,38,40,41,42,44

Table III
Mean head widths for later instar larvae of the three developmental types. Values in parentheses are growth ratios (GR[N] = HW[N]/HW[N-1])

Instar	Mean head widths (mm)		
	12-instar (n=5)	*13-instar* (n=12)	*14-instar* (n=1)
9	1.95 (1.27)	1.86 (1.22)	1.68 (1.12)
10	2.36 (1.21)	2.26 (1.22)	2.02 (1.26)
11	2.89 (1.22)	2.67 (1.18)	2.46 (1.20)
12	3.46 (1.20)	3.08 (1.15)	2.96 (1.20)
13		3.66 (1.19)	3.44 (1.16)
14			3.82 (1.11)

The results of the character analysis for specimens of the 13-instar type from the Cave & Basin are given in Table II. The number of antennomeres was constant within each instar, but all other characters showed intra-instar variation which increased with instar. Values for the 12- and 14-instar types fell within the ranges for the corresponding instars in Table II except for head-widths of late stage larvae, which are given in Table III. There was no increase in head width during an instar once expansion of the new cuticle had occurred about 10 min after ecdysis. There was no significant difference between male and female head widths in any instar, but there were differences ($p < 0.05$) between populations in instars 10-12 at 20° C, individuals from Deep Creek being smaller than those from Cave & Basin (Tab. IV). At 15 and 20° C, head-widths of earlier instars from Deep Creek were larger than from Cave & Basin, although these differences were not statistically significant, while at 25° C the two populations were the same (Tab. IV)

If we assume that the head widths of the small sample of instar 9 and 10 larvae given in Table III are indicative of developmental type, then we can predict the developmental type of any individual reared to instar 9 or 10. An analysis of this type leads to the prediction that the number of instars increases with temperature (Tab. V).

Table IV
Mean head width values (x̄ ± 1 SE) for each instar at temperatures of 15, 20 and 25° C. (Values in parentheses represent sample size. — C.B. = Cave & Basin; D.C. = Deep Creek)

Instar	Locality	Temperature (° C) 15	20	25
	C.B.	0.36±0.01 (18)	0.36±0.01 (20)	0.36±0.01 (20)
2	D.C.	0.36±0.01 (20)	0.36±0.01 (20)	0.36±0.01 (20)
	C.B.	0.46±0.01 (43)	0.46±0.01 (43)	0.48±0.01 (55)
3	D.C.	0.47±0.01 (23)	0.46±0.01 (23)	0.47±0.01 (20)
	C.B.	0.58±0.01 (38)	0.59±0.01 (38)	0.63±0.01 (44)
4	D.C.	0.60±0.01 (20)	0.60±0.01 (22)	0.63±0.01 (19)
	C.B.	0.76±0.01 (31)	0.76±0.01 (36)	0.80±0.01 (40)
5	D.C.	0.79±0.01 (15)	0.79±0.01 (20)	0.79±0.01 (14)
	C.B.	0.97±0.01 (30)	0.97±0.01 (35)	1.01±0.01 (37)
6	D.C.	1.02±0.02 (14)	1.02±0.02 (20)	1.00±0.02 (13)
	C.B.	1.26±0.02 (28)	1.23±0.02 (34)	1.25±0.01 (27)
7	D.C.	1.27±0.03 (12)	1.25±0.02 (19)	1.23±0.02 (12)
	C.B.	1.56±0.02 (25)	1.50±0.02 (33)	1.51±0.02 (24)
8	D.C.	1.62±0.01 (10)	1.52±0.03 (15)	1.49±0.03 (8)
	C.B.	1.91±0.03 (23)	1.83±0.02 (29)	1.82±0.02 (17)
9	D.C.	2.00±0.02 (10)	1.77±0.02 (11)	1.81±0.02 (5)
	C.B.	2.33±0.03 (20)	2.34±0.03 (26)	2.01±0.03 (13)

Table IV (continued)

Instar	Locality	Temperature (° C) 15	20	25
10	D.C.	2.43±0.02 (10)	2.04±0.03 (11)	2.01±0.05 (4)
	C.B.	2.79±0.04 (13)	2.69±0.04 (18)	2.43±0.04 (6)
11	D.C.	2.89±0.05 (6)	2.46±0.04 (11)	2.47±0.07 (3)
	C.B.	3.30±0.07 (10)	3.12±0.06 (9)	3.00±0.02 (3)
12	D.C.		2.92±0.02 (4)	2.95 (1)
	C.B.	3.52±0.04 (4)	3.56±0.05 (5)	
13	D.C.		3.38 (2)	
14	C.B.		3.82 (1)	

Table V

Frequency of developmental types at temperatures of 15, 20 and 25° C. (Numbers outside parentheses represent observed frequencies, while those in parentheses are predicted percentage values based on head width data for instar 9 or 10)

Developmental type	Temperature (° C) *Cave & Basin* 15°	20°	25°	*Deep Creek* 15°	20°	25°
12	5(40)	0(26)	(0)	(40)	(0)	(0)
13	11(55)	2(61)	(36)	(60)	(14)	(40)
14	0(5)	1(13)	(64)	(0)	(86)	(60)

DISCUSSION

The ellipsoidal shape of the eggs of *Argia vivida* is typical of the Zygoptera, which oviposit endophytically, and although few observations on hatching have been published, the pattern appears similar to those recorded to date, including the attachment of the instar 1 cuticle to the egg shell (PILON, 1982). The functions of the prolarva are to escape from material surrounding the egg, and to reach water safely when the egg has been laid some distance from it (CORBET, 1962). However, where eggs are oviposited singly in the larval habitat, as in *A. vivida,* the molt to the second instar can occur during eclosion, although under adverse conditions it may be advantageous for the prolarva to leave the egg, as it does in *A. vivida* at 35° C, and search for a more favorable habitat.

The large amount of intra-instar variation in larval characters appears typical of Zygoptera (PILON & RIVARD, 1979; PILON & FONTAINE, 1980; PILON & MASSEAU, 1983), and only instars 1, 2, 3, and the final (F) of *A. vivida* can be identified with certainty. Head widths can be used to construct a series of instar boundaries for the most common developmental type of 13 instars (Tab. VI). The fit of all laboratory-reared larvae to this scheme varied from 100% for instar 2 to 70% for instars 9-12. Instars 2 and 3 can be identified by the number of antennomeres, and the final instar is best identified by metathoracic wing-pad length, which is > 4 mm.

Table VI
Mean head widths and class boundaries for the 13-instar developmental type

Instar	Head width (mm) ($\bar{x}$ ± 1SD	Class boundaries	% fit
2 (F-11)	0.36 ± 0.01	0.34 - 0.38	100
3 (F-10)	0.47 ± 0.03	0.39 - 0.54	95
4 (F-9)	0.61 ± 0.04	0.55 - 0.71	85
5 (F-8)	0.78 ± 0.05	0.72 - 0.86	85
6 (F-7)	0.99 ± 0.07	0.87 - 1.13	80
7 (F-6)	1.25 ± 0.09	1.14 - 1.35	80
8 (F-5)	1.52 ± 0.10	1.36 - 1.65	80
9 (F-4)	1.86 ± 0.13	1.66 - 2.00	70
10 (F-3)	2.26 ± 0.25	2.01 - 2.40	70
11 (F-2)	2.67 ± 0.21	2.41 - 2.95	70
12 (F-1)	3.08 ± 0.17	2.96 - 3.60	70
13 (F)	3.66 ± 0.11	3.20 - 4.30	*

* Final instar recognized by wing-pad length; boundaries given are actual range.

The instar boundaries given here are similar to those determined by PRITCHARD & PELCHAT (1977), although ours are consistently lower. Pritchard & Pelchat did not recognize the existence of developmental types and this, of course, contributed to the difficulties they had in defining instars. Also, one of the methods they used was to assume a constant growth ratio of 1.19 and work backwards from the mean head width of field-collected final instar larvae. We have now shown that the growth ratio is not constant, but decreases as larvae grow.

The average growth ratio in *A. vivida* is 1.24, within the range for hemimetabolous insects found by COLE (1980), who gave a median growth ratio of 1.27 for hemimetabolous insects and 1.52 for holometabolous insects. Cole suggested that this difference was related to the fact that holometabolous larvae are adapted to ephemeral habitats, best exploited by insects which mature rapidly and have few instars, wheras hemimetabolous insects appear better adapted to exploit more temporally stable habitats, a strategy which does not require high growth ratios and thus these insects have a larger number of instars. PRITCHARD & MUTCH (1984) argued that molting carries risks and thus there would be advantage in a reduction of the number of molts during the life cycle and consequently higher growth ratios. The reduction in sclerotized parts in holometabolous insects has undoubtedly allowed larger growth ratios.

The increase in number of instars with temperature has been observed for several insects (WIGGLESWORTH, 1972), including odonates (SCHALLER, 1960). Since size of final instar larvae also increases with number of instars (also found by INGRAM & JENNER (1976) in a zygopteran, by KHOO (1964) in a stonefly, and by FREMLING, 1973, in a mayfly) then size also will increase with temperature, at least over the range 15 to 25° C. Size was used as a measure of fitness by VANNOTE & SWEENEY (1980) when they proposed that there is a temperature to which aquatic insects are best adapted. Thus, on this criterion, 25° C would appear to be more favorable for the development of *A. vivida* than are lower temperatures. However, we do not know whether larger larval size is translated into higher adult fitness, nor do we know whether there is a trade-off with reduced fitness due to the extra molts.

Finally, the elucidation of these life-cycle patterns in the laboratory allows us to propose an explanation for the observation made by PRITCHARD & PELCHAT (1977) that final instar larvae at the Cave & Basin were larger in April through June than in August. These authors suggested that the small individuals in August may not have been encountered in previous samples because they may have been living in the colder, marginal areas of the habitat which were not sampled. If this were so, then they would have developed more slowly, completed development in fewer instars, and thus have been smaller than the larvae measured in the spring.

ACKNOWLEDGEMENTS

We thank RAMNIK ARORA and JANIS LEMISKI for technical assistance, KELVIN CONRAD and MICHAEL BENTON for reading the manuscript, and the Natural Sciences & Engineering Research Council of Canada for financial support.

REFERENCES

COLE, B.J., 1980. Growth rates in holometabolous and hemimetabolous insects. *Ann. ent. Soc. Am.* 73: 489-491.

CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.

FREMLING, C.R., 1973. Environmental synchronization of mass Hexagenia bilineata

(Ephemeroptera) emergences from the Mississippi River. *Int. Ver. theor. angew. Limnol.* 18: 1521-1526.

HINTON, H.E., 1981. *Biology of insect eggs,* Vol. I. Pergamon Press, Oxford-New York.

INGRAM, B.R. & C.E. JENNER, 1976. Influence of photoperiod and temperature on development time and number of molts in nymphs of two species of Odonata. *Can. J. Zool.* 54: 2033-2045.

KHOO, S.G., 1964. Studies on the biology of Capnia bifrons (Newman) and notes on the diapause in the nymphs of this species. *Gewäss. Abwäss.* 34/35: 23-30.

LINLEY, J.R. & D.G. EVANS, 1971. Behaviour of Aedes taeniorhynchus larvae and pupae in a temperature gradient. *Entomologia exp. appl.* 14: 319-332.

PILON, J.-G., 1982. Notes on oviposition and embryonic development of Enallagma ebrium (Hagen) and E. vernale Gloyd in Quebec (Zygoptera: Coenagrionidae). *Odonatologica* 11: 45-52.

PILON, J.-G. & R. FONTAINE, 1980. Étude morphologique des larves de Enallagma ebrium (Hagen) (Zygoptera: Coenagrionidae). *Odonatologica* 9: 155-171.

PILON, J.-G. & M.J. MASSEAU, 1983. Morphologie externe des larves de Enallagma hageni (Walsh) (Odonata: Coenagrionidae). *Odonatologica* 12: 125-140.

PILON, J.-G. & D. RIVARD, 1979. Étude morphologique des larves de Enallagma vernale Gloyd, elevées en laboratoire (Zygoptera: Coenagrionidae). *Odonatologica* 8: 285-299.

PRITCHARD, G., 1980. The life cycle of Argia vivida Hagen in the northern part of its range (Zygoptera: Coenagrionidae). *Odonatologica* 9: 101-106.

PRITCHARD, G., 1982. Life-history strategies in dragonfly and the colonization of North America by the genus Argia (Odonata: Coenagrionidae). *Adv. Odonatol.* 1: 227-241.

PRITCHARD, G. & C. MUTCH, 1984. Intermolt cuticle and muscle growth in Tipula larvae (Insecta, Diptera). *Can. J. Zool.* 62: 1351-1354.

PRITCHARD, G. & B. PELCHAT, 1977. Larval growth and development of Argia vivida (Odonata: Coenagrionidae) in warm sulphur pools at Banff, Alberta. *Can. Ent.* 109: 1563-1570.

SCHALLER, F., 1960. Étude de développement post-embryonnaire d'Aeschna cyanea Müll. *Annls Sci. nat.* (Zool. Biol. Anim.) 2: 741-856.

VANNOTE, R.L. & B.W. SWEENEY, 1980. Geographic analysis of thermal equilibria; a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.* 115: 667-695.

WHITEHOUSE, F.C., 1941. British Columbia dragonflies (Odonata) with notes on distribution and habits. *Am. Midl. Nat.* 26: 488-557.

WIGGLESWORTH, V.B., 1972. *The principles of insect physiology,* 7th ed., Chapman & Hall, London.